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Widening the net: spatio-temporal variability in the krill population structure across the Scotia Sea

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Abstract

Resolving the spatial variability in the population structure of Antarctic krill (*Euphausia superba*) requires a synoptic sample, as in the design of the CCAMLR 2000 Survey. However, this approach is not appropriate for assessing temporal variability. The size of krill in the diet of Antarctic fur seals (*Arctocephalus gazella*) has been shown to provide a good representation of the temporal changes in the krill population structure from within their foraging area. At Cape Shirreff, South Shetland Islands, krill in nets had modal size classes of 46–48 mm and 52–54 mm in length and appeared to reflect the presence of larger krill offshore and smaller krill inshore; krill in the diet of fur seals contained both modes, indicating that the foraging area of fur seals integrated the spatial variability in the krill population. At Signy Island, South Orkney Islands, krill in nets and fur seal diets had a modal size class of 52 mm when sampled simultaneously; however, krill in the diet of seals showed a decline in size later in the season with an overall mode of 48 mm. At Bird Island, South Georgia, there was little overlap between net samples, with a modal size class of 30–40 mm, and fur seal diets, with distinct modes of 44 and 54 mm; and there was also much greater spatial variability in the size of krill in these net samples than in those from the other two locations. Extending the comparison of krill size in the diet of seals, to include spatially congruent net samples collected immediately prior to the CCAMLR 2000 Survey, showed almost complete overlap and indicated an even greater spatial variability in the krill population structure at South Georgia. Interactions between the oceanographic transport and enhanced growth rates of krill at South Georgia may combine to produce a higher degree of spatial variability in the krill population compared to other locations and this may limit the use of differences in krill length as an indicator of their provenance. This study underlines the importance of using data from multiple sources when considering large-scale krill population dynamics; information that is crucial to the effective management of the commercial exploitation of krill.

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1. Introduction

The size structure of the population of Antarctic krill (*Euphausia superba*) in the Scotia Sea is the product of a complex set of interactions between physical and biological processes that combine to produce a high level of spatial and temporal variability (Murphy et al., 1998). In order to investigate the causes and consequences of variability in the krill population, it is essential to consider the relative contributions from the different sources of variability. Resolution of the variability into its spatial and temporal components requires a combination of analyses at appropriate scales of measurement. To assess the spatial component, simultaneous samples of the krill population are required across the entire area over which that population occurs, whereas an assessment of the temporal component might best be addressed through repeat sampling at a single site over a longer period of time. The design of the CCAMLR 2000 Survey provides a detailed 'snapshot' of the biomass, distribution, and size structure of the krill population across the Scotia Sea (Trathan et al., 2001). Since logistic and financial constraints prevent replicate ship-based surveys as a means of assessing temporal variability in the Scotia Sea krill population, an alternative approach to ship-based sampling was required to address the temporal variation.

Long-term monitoring of the size of krill in the diet of krill-dependent predators, such as Antarctic fur seals (*Arctocephalus gazella*), has proved very effective in revealing temporal changes in the population structure of krill at South Georgia, both within and between years (Murphy and Reid, 2001; Reid, 2001; Reid et al., 1999). Since Antarctic fur seals are found on all island groups within the Scotia Sea (Boyd, 1993), extending the diet sampling protocols developed at South Georgia to other sites in the Scotia Sea was considered a potential mechanism for examining temporal variation in krill population size structure at different geographical locations.

During the design phase of the CCAMLR 2000 Survey, intensive net sampling was planned in the vicinity of South Georgia, the South Orkney Islands, and the South Shetland Islands (Trathan et al., 2001). Located in each of these regions are land-based CCAMLR Ecosystem Monitoring Programme (CEMP) sites, where Antarctic fur seals are known to occur during summer. This presented an ideal opportunity to collect samples of krill from the diets of seals before, during, and after the periods of ship-based net sampling. Integrating these time series of samples from different locations with data from the synoptic ship-based survey was considered a potentially suitable approach for examining the spatial and temporal variation in the krill population of the Scotia Sea.

The aim of this paper is to use the data on the length–frequency distribution of krill in the diet of Antarctic fur seals at the three locations over the period around the CCAMLR 2000 Survey: (1) to establish the level of concordance between the dietary and net samples; (2) to investigate temporal change in the krill population structure over the summer; and (3) to consider the potential contributions of temporal and spatial variation to the overall variability in the size structure of the Scotia Sea krill population.

2. Methods

Faeces (scats) of Antarctic fur seals were collected at regular intervals between mid-December 1999 and late March 2000 (or for as long as possible between these dates depending upon logistic constraints) at Cape Shirreff (Livingston Island, South Shetland Islands; 62°28′S, 60°46′W), Signy Island (South Orkney Islands; 60°42′S, 45°38′W), and Bird Island (South Georgia; 54°00′S, 38°03′W) (see Fig. 1). There are colonies of breeding fur seals at Cape Shirreff and Bird Island (Boyd, 1993), whereas on Signy Island the fur seal population consists almost entirely of non-breeding sub-adult and adult male seals (Hodgson and Johnston, 1997). Only whole, fresh scats were collected, and all sorting and krill measurement followed the methods of Reid and Arnould (1996). All ship-based net sampling was conducted using RMT8 scientific research nets and krill lengths in net samples were measured for a sub-sample of up to 200 krill following the protocol outlined in

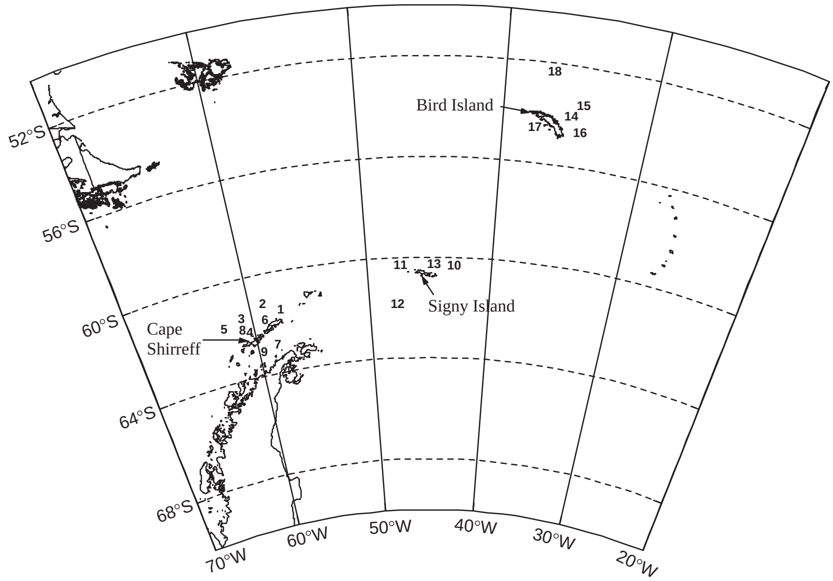

Fig. 1. Location of the land-based sampling sites (shown by the arrow) and net hauls (corresponding to the net number in Table 1).

(Siegel et al., 2004). Krill from scats collected within the same seven-day period were considered as a single sample, as were those krill from individual net hauls. All composite length–frequency distributions use the mean proportions in each 2 mm size class from 20 to 68 mm in order to standardize with respect to sample size.

3. Results

3.1. Samples sizes

A total of 2521 krill were measured from 96 scats collected in the South Shetland Islands between 5 January and 8 March, and 1011 krill were measured from the nine net hauls. At the South Orkney Islands, 2366 krill were measured from 128 scats collected between 12 January and 22 March and 546 from four net hauls. Between 22 December and 22 March, 932 krill were measured from 140 scats and 448 krill were measured from the five net hauls at South Georgia. Table 1 provides details of the location, time of sampling, and sample size of krill obtained in the nets. Table 2 provides the corresponding data for scats.

3.2. Population size structure

3.2.1. South Shetland Islands

The modal size class in the composite length–frequency distribution of dietary krill for fur seals from Cape Shirreff was 52 mm, as was the modal size class in the composite length–frequency distribution for krill in net samples from the South Shetland Islands region; in both cases 86% of krill were between 46 and 56 mm in length (Fig. 2). In the weekly scat samples there was evidence of two distinct modes, at 46–48 mm and 52–54 mm, both of which were present throughout the entire sampling period (Fig. 3), while a mode of 56 mm was present only during the weeks prior to the collection of the net hauls. There was a decrease in the mean size of krill between January and March ($F_{(1,10)} = 18.19$; $P = 0.003$), which was reflected in a significant decline in the proportion of krill $\geqslant 52$ mm over the same period ($F_{(1,10)} = 22.43$; $P = 0.001$). The individual net samples suggest that the modal size class of 52–54 mm was prevalent offshore (nets 2, 3, and 5), while smaller krill, with a modal size class of 48 mm, dominated inshore catches (nets 1,4, 6, 7, and 9) (Fig. 4).

Table 1
The station number, location, water depth, time and number of krill measured in the net hauls

Net	Station	Longitude	Latitude	Depth (m)	Date	Time (utc)	*N*	Region
1	KM5032	−58.2007	−61.7510	287	30 Jan	1705	30	SSI
2	KM5033	−59.6093	−61.3737	3465	31 Jan	0334	165	SSI
3	KM5035	−61.6577	−61.7680	4792	01 Feb	0336	158	SSI
4	KM5036	−61.1900	−62.4055	—	01 Feb	1425	164	SSI
5	KM5037	−63.2400	−62.0263	4053	02 Feb	0334	45	SSI
6	KM1523	−59.5888	−62.1078	98	25 Jan	0352	155	SSI
7	KM1524	−59.0902	−63.0907	182	25 Jan	1619	154	SSI
8	JR1634	−61.2177	−62.3020	225	07 Feb	0300	111	SSI
9	JR1640	−60.3995	−63.2615	480	11 Feb	1511	29	SSI
10	JR723	−43.5693	−60.6027	1870	30 Jan	1152	151	SOI
11	KM918	−47.9097	−60.5028	1761	12 Jan	0331	89	SOI
12	KM919	−48.3007	−62.1230	3295	12 Jan	1540	158	SOI
13	YU4030	−45.1997	−60.4753	300	30 Jan	0328	148	SOI
14	YU3003	−35.8182	−54.3353	225	14 Jan	1511	132	SG
15	YU3004	−35.0600	−53.8518	3560	15 Jan	0359	88	SG
16	KM303	−35.0760	−54.9063	143	12 Jan	0227	164	SG
17	JR413	−37.7658	−54.7717	293	25 Jan	0149	41	SG
18	JR415	−37.2818	−52.3862	2540	26 Jan	0153	23	SG

SSI: South Shetland Islands; SOI: South Orkney Islands; SG: South Georgia.

Table 2
The date (end of the seven-day sampling period), location, and sample sizes of krill measured in the diet of Antarctic fur seals

Date	Week number	SSI	SOI	SG
22 Dec 1999	1			60
29 Dec 1999	2			21
05 Jan 2000	3	292		64
12 Jan 2000	4	271	53	90
19 Jan 2000	5	274	218	77
26 Jan 2000	6	325	37	80
02 Feb 2000	7	90	280	87
09 Feb 2000	8	480	238	73
16 Feb 2000	9	80	127	82
23 Feb 2000	10	425	90	70
01 Mar 2000	11	137	318	58
08 Mar 2000	12	147	147	58
15 Mar 2000	13		502	72
22 Mar 2000	14		356	40

SSI: South Shetland Islands; SOI: South Orkney Islands; SG: South Georgia.

3.2.2. South Orkney Islands

The composite length–frequency distribution of dietary krill for fur seals from Signy Island had a modal size class of 48 mm, with 95% of krill between 44 and 54 mm in length, while the composite length–frequency distribution for krill in net samples from the South Orkney Islands region had a modal size class of 52 mm, with 79% of krill between 44 and 54 mm in length (Fig. 5). In the weekly scat samples there was evidence of a distinct mode at 52 mm at the beginning of the series and a distinct mode at 48 mm at the end (Fig. 6). There was a gradual change, involving some oscillation between the larger and the smaller mode, such that during the sampling period there was a decline in the mean size of krill over the sampling period ($F_{(1,11)} = 29.98$; $P < 0.001$). There was a very similar size structure of krill in the individual net samples, each of which had a mode of 52 mm and with relatively few krill smaller than 44 mm (Fig. 7).

3.2.3. South Georgia

The composite length–frequency distribution of dietary krill for fur seals from Bird Island contained two distinct modes, at 44 and 54 mm, whereas the composite length–frequency distribution for krill in net samples from the South

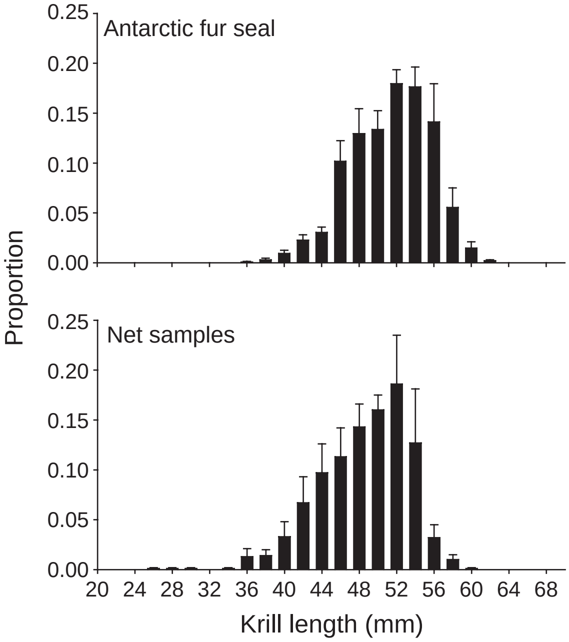

Fig. 2. Composite length–frequency data for krill in the diet of Antarctic fur seals at Cape Shirreff from January to March 2000 and in net hauls from the region of the South Shetland Islands during the CCAMLR 2000 Survey.

Georgia region had an indistinct mode between 30 and 40 mm (Fig. 8). In the weekly scat samples krill representing the smaller mode (44 mm) were present throughout the sampling period; however, the larger mode (54 mm) was only present during the period up to late January (Fig. 9). The individual net hauls showed considerable variability in terms of krill size, with modal size classes ranging from 28 to 40 mm (Fig. 10).

4. Discussion

In the South Shetland Islands, the length–frequency distribution of krill from Antarctic fur seals and nets showed extensive overlap indicating that the variability reflected in the spatially explicit net samples also was reflected within the foraging areas of the fur seals. At the South Orkney Islands, the dominance of the 48 mm size class in the diet of Antarctic fur seals compared to the 52 mm in the net samples was a consequence of the shift in the modes from 52 to 48 mm over the course of the season. Thus, for most of the period after the net samples were collected, the 48 mm size class predominated in the diet of seals and this is reflected in the composite length–frequency distribution. However, comparison of the length–-frequency distributions of krill from Antarctic fur seals and nets from the same time period showed extensive overlap with a modal size of 50–52 mm. At South Georgia, there was little overlap in the length–frequency distributions of krill from nets and Antarctic fur seals, even when comparisons were restricted to samples collected at exactly the same time. Whilst 80% of krill from nets were of 40 mm or less only, 10% of those from Antarctic fur seals were of this size; in addition, there was a distinct mode at 54 mm in the diet of Antarctic fur seals, which was not represented in any of the net samples.

Interpretation of these results is constrained by the limitation of the sampling regimes, in particular the small number of net samples undertaken in the region of the South Orkney Islands and at South Georgia; the different part of the fur seal population present in the South Orkney Islands; and the single land-based sampling site in each of the three regions. Nevertheless, at both the South Shetland Islands and South Orkney Islands there was a relatively high level of overlap in the sizes of krill taken by Antarctic fur seals and nets, which probably reflects the dominance of large krill in the population since these are effectively fully sampled by Antarctic fur seals (Murphy and Reid, 2001). At the South Shetland Islands, there was a relatively well-defined spatial variability and evidence of a relatively small temporal change. This temporal change may reflect changes in the foraging distribution of seals leading to the sampling of different components of the krill population; however, in previous studies of the krill in this region there has been evidence of distinct changes in the age–composition and distribution of krill (Lascara et al., 1999). At the South Orkney Islands, whilst there was also a temporal change in size structure, there was no evidence of spatial heterogeneity, at least during the period of net sampling. This contrasts with the situation at South Georgia where there was far less

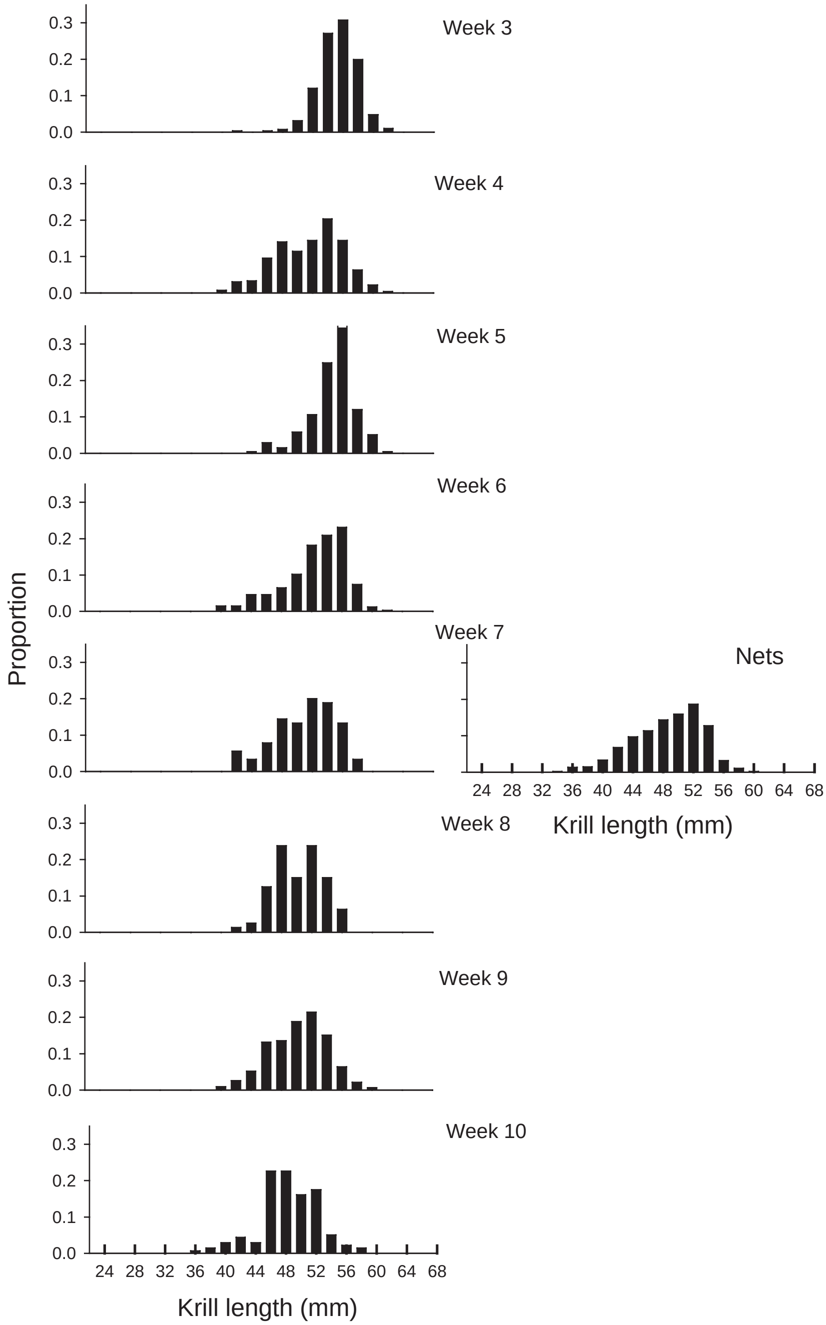

Fig. 3. Length–frequency data for krill in the diet of Antarctic fur seals at Cape Shirreff for weeks 3–10 with the composite length–frequency data for net hauls taken from the region of the South Shetlands Islands during the CCAMLR 2000 Survey aligned to week 7, the period of simultaneous sampling.

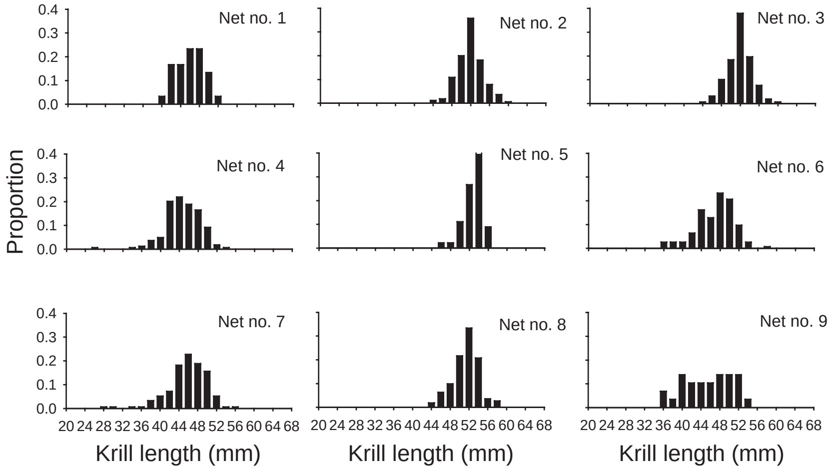

Fig. 4. Length–frequency data for krill in net hauls from the region of the South Shetland Islands during the CCAMLR 2000 Survey. (Net numbers as in Table 1.)

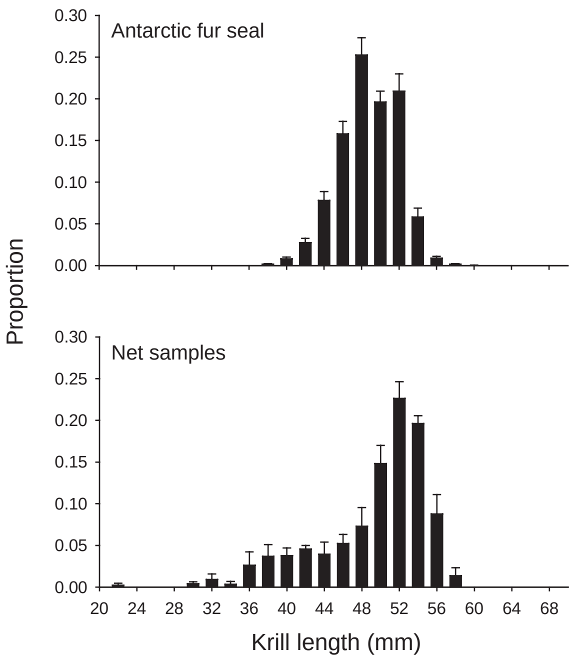

Fig. 5. Composite length–frequency data for krill in the diet of Antarctic fur seals at Signy Island from January to March 2000 and in net hauls from the region of the South Orkney Islands during the CCAMLR 2000 Survey.

overlap in the sizes of krill taken by nets and seals. There was also evidence of a distinct temporal change in the size of krill taken by Antarctic fur seals and a high degree of spatial variability in the regional net samples. This spatial variability at South Georgia had a less well-defined pattern, especially with respect to bathymetry, compared to the South Shetland Islands. Thus, it appears that at the South Shetland Islands and the South Orkney Islands, there was a relatively similar pattern of change in krill population structure, and in both cases, the krill population was dominated by large krill throughout the sampling period. In contrast, at South Georgia, the net samples indicated extensive spatial differences and temporal differences were reflected in the samples from Antarctic fur seals; together these produced the greatest amount of variability in population structure and the lowest level of overlap between the samples from nets and Antarctic fur seals.

The extent of overlap between the krill taken by Antarctic fur seals and nets will depend to some extent on the nature of the krill population structure; when the population is dominated by large krill there will be a high level of overlap, whereas this overlap may well decrease when small krill dominate (Reid et al., 1999). In 2000, the dominance of large krill in the population at both the South Shetland Islands and the South Orkney Islands resulted in a high degree of overlap. Initially, it would appear that the lack of overlap at South Georgia reflects the dominance of small

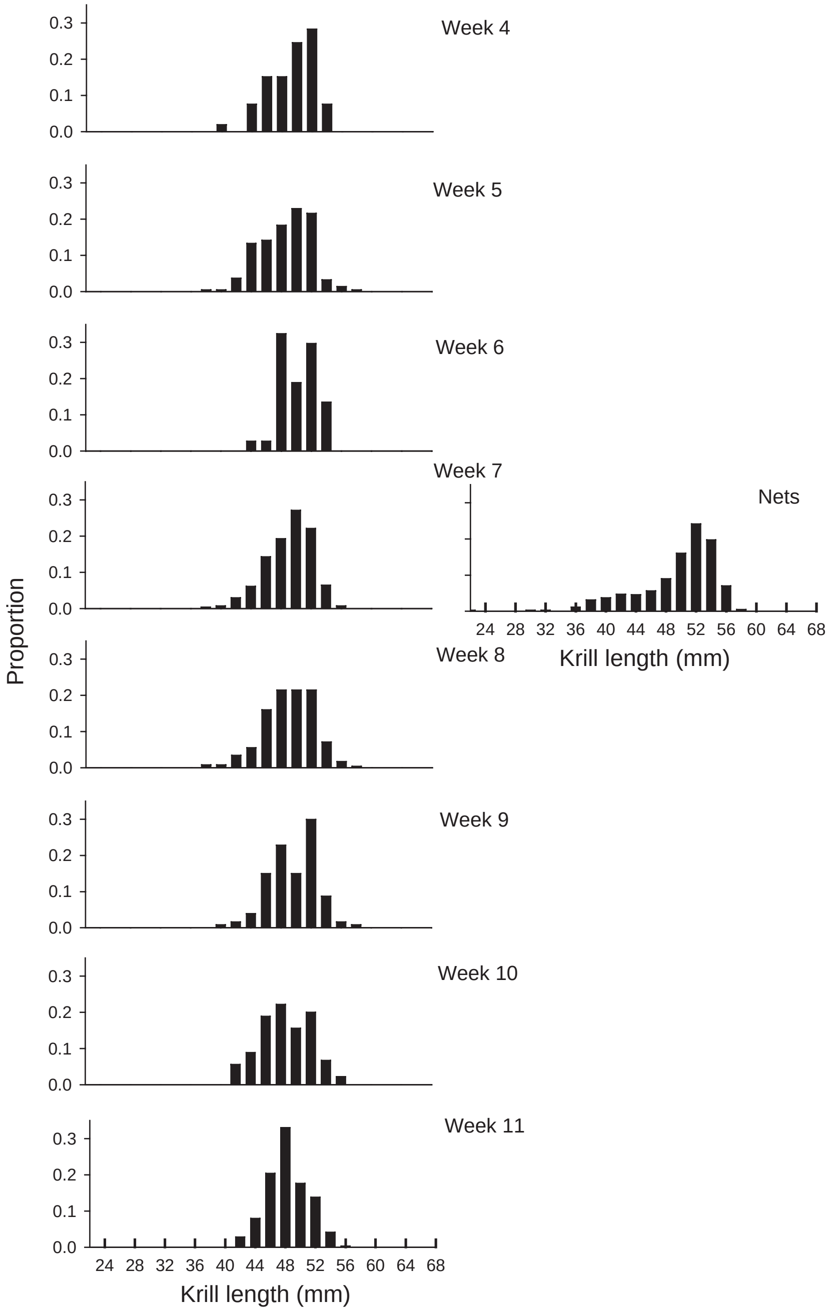

Fig. 6. Length–frequency data for krill in the diet of Antarctic fur seals at Signy Island for weeks 4–11 with the composite length–frequency data for net hauls taken from the region of the South Orkney Islands during the CCAMLR 2000 Survey aligned to week 7, the period of simultaneous sampling.

krill in that population. However, previous comparisons of krill in the diet of Antarctic fur seals and nets have demonstrated the importance of making the comparison at appropriate scales, both in terms of the temporal and spatial dimension (Reid et al., 1999). While the present data can be

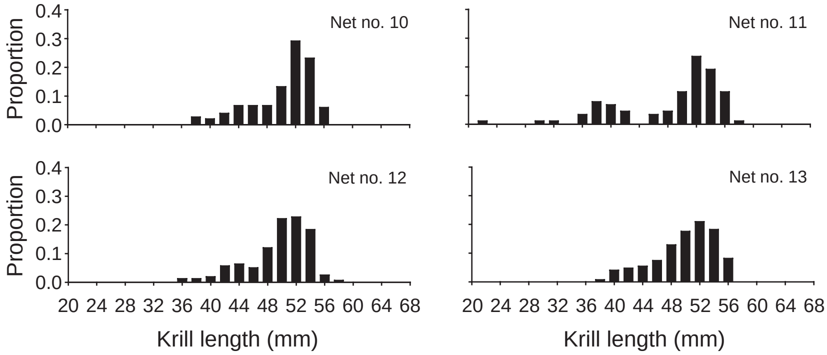

Fig. 7. Length–frequency data for krill in net hauls from the region of the South Orkney Islands during the CCAMLR 2000 Survey. (Net numbers as in Table 1.)

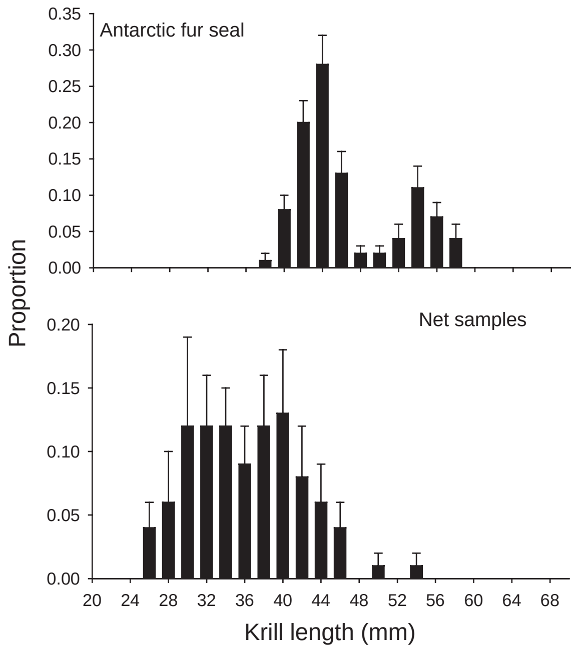

Fig. 8. Composite length–frequency data for krill in the diet of Antarctic fur seals at Bird Island from January to March 2000 and in net hauls from the region of South Georgia during the CCAMLR 2000 Survey.

compared at a simultaneous temporal scale (i.e. were collected at the same time), all the net samples from the South Georgia region (Fig. 1) were taken to the east of the foraging area used by lactating female Antarctic fur seals from Bird Island (Barlow et al., 2002; Boyd et al., 1998). However, the length–frequency distribution of krill from within the foraging area of female Antarctic fur seals, collected immediately prior to the CCAMLR 2000 Survey (data from Sushin et al., 2000), overlaps almost completely with the length–frequency distribution in the diet of Antarctic fur seals collected during the present study (Fig. 11). Thus, when comparisons are made at appropriate scales, the sizes of krill in the diet of Antarctic fur seals shows good agreement with the sizes of krill taken in nets.

In this study, the high level of agreement between the size of krill in the diet of Antarctic fur seals and nets probably relates to the dominance of large individuals in the krill population within the foraging range of those seals. However, in situations where this is not the case, i.e., when there is a dominance of small krill, it is essential to account for any size selectivity either by including samples from other krill predators that do not have the same size selectivity (e.g., penguins; Reid et al., 1999) or by applying quantitative selectivity functions (see Murphy and Reid, 2001) in order to obtain the most accurate representation of the size structure of the krill population.

The spatial variability in the size structure of the krill population at South Georgia is consistent with previous analyses in which larger krill predominated in samples taken to the west of the island and smaller krill in the east (Watkins et al., 1999). It has been suggested that this spatial variation in krill size may be due to differing source regions; the larger krill at the western end of the island are thought to be associated with the

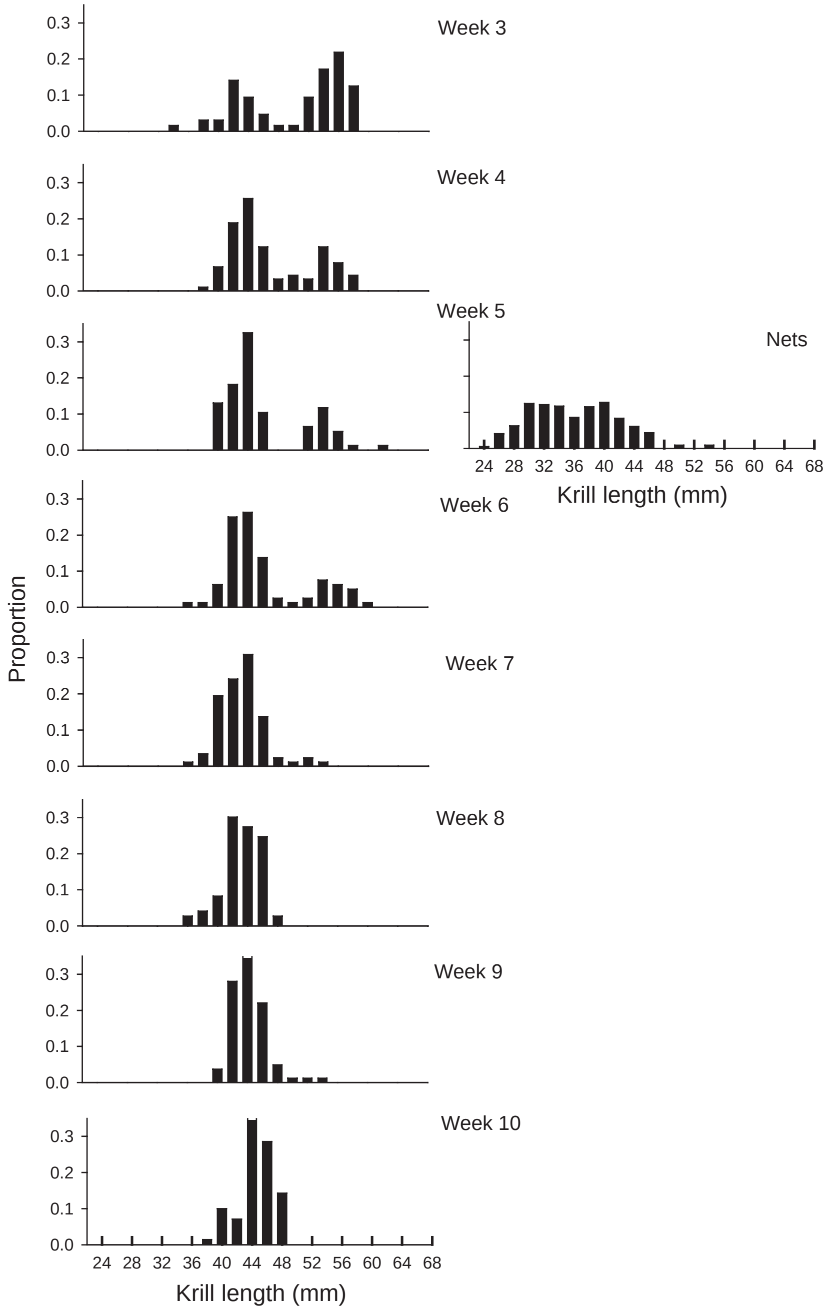

Fig. 9. Length–frequency data for krill in the diet of Antarctic fur seals at Bird Island for weeks 3–10 with the composite length–frequency data for net hauls taken from the region of South Georgia during the CCAMLR 2000 Survey aligned to week 7, the period of simultaneous sampling.

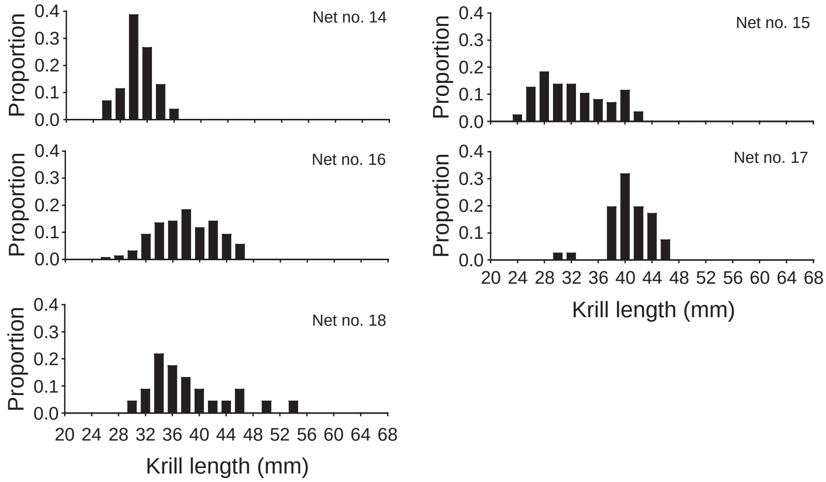

Fig. 10. Length–frequency data for krill in net hauls from the region of South Georgia during the CCAMLR 2000 Survey. (Net numbers as in Table 1.)

Antarctic Circumpolar Current and to originate in the southern Scotia Sea and the Antarctic Peninsula region, while the smaller krill, at the eastern end of the island, have been described as originating in the Weddell Sea (Watkins et al., 1999). An alternative scenario is emerging as a result of increasing interest in the role of the Southern Antarctic Circumpolar Current Front in the transport of krill into the South Georgia region (e.g. Murphy et al., 1998; Thorpe et al., 2002). This has the potential to introduce krill into the eastern end of the system from where they are transported westward. It may be that the interactions of a relatively high growth rate for krill at South Georgia (Reid, 2001) and oceanographic transport around the island combine to produce a high level of spatial variability in size structure in a single population. The differences in the modal sizes in the net samples from South Georgia, ranging from 28 to 40 mm, with the smallest in the east and modal size generally increasing westward, is consistent with krill of the same size class entering the system and being transported through a region in which they experience enhanced growth rates. In a complex oceanographic system, such as those associated with oceanic islands, a 'synoptic' sample across the region would probably reveal a high degree of spatial variability in krill size. Nevertheless, those krill that have been exposed to the enhanced growth conditions for longer and by analogy have been transported further through the region would be expected to be more abundant further west. Conversely, those krill in the eastern region would be smaller having been in the 'system' for a shorter period of time.

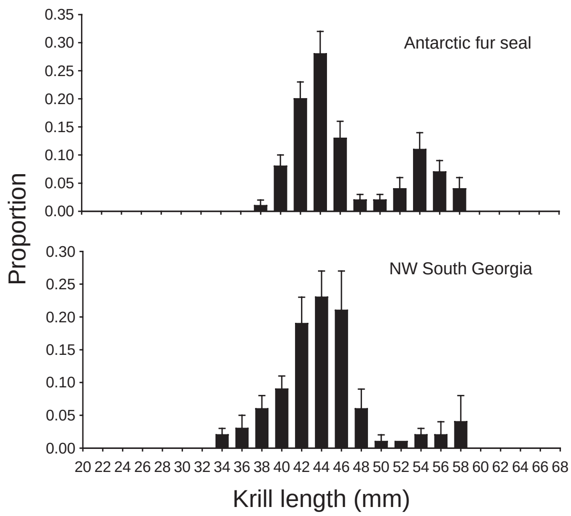

Fig. 11. Composite length–frequency distribution of krill in the diet of Antarctic fur seals at Bird Island from January to March 2000 and in nets from the AtlantNIRO/BAS research cruise at South Georgia during January 2000 (data from Sushin et al., 2000).

The greater temporal variation in the krill taken by Antarctic fur seals at South Georgia may to some extent also reflect the locally high krill mortality rate (Murphy and Reid, 2001), which is manifested in a reduction in the abundance of the krill in the larger mode during the course of the summer. The potential interaction between demographic parameters (i.e. growth and mortality) and transport within the South Georgia region has the potential to produce a very high degree of spatial and temporal variability in the population structure of krill around the island. Therefore, it may be inappropriate to use differences in the size of krill at different locations around the island as an indicator of different source regions for these krill. This does not mean that the multiple source region hypothesis should be rejected, simply that it should not be based on the size of krill alone and that some other indicator of the provenance of these krill is required.

Given the interactions of spatial and temporal variability in the krill population over the whole of the Scotia Sea, it is important to consider the potential limitations of different sampling protocols. Watkins et al. (1990) showed that small-scale heterogeneity can have a marked effect on the sample sizes required to characterize the krill population and suggested that a minimum of 20 net hauls would be required to remove the effects of this heterogeneity at a regional scale. However, the requirement for a near-synoptic acoustic determination of krill biomass precluded the possibility of net sampling at that intensity during the CCAMLR 2000 Survey. It is therefore important to consider what collateral information may be available on the composition of the krill population either from predators, or alternative net samples such as from commercial fisheries, when considering the regional population dynamics of krill.

Whilst there was little evidence of krill smaller than 42 mm in the net samples obtained during the CCAMLR 2000 Survey in the Antarctic Peninsula region, smaller size classes of krill were present in samples from a research cruise in December 1999 (Hewitt et al., 2004). Similarly, net hauls collected during the CCAMLR 2000 Survey at South Georgia did not contain krill with a modal size of 52–54 mm; yet this portion of the krill population was present in the diet of Antarctic fur seals and in net hauls from an associated krill survey (Fig. 11). Therefore, consideration of the regional population dynamics should include information from all available sources, particularly where such studies indicate the presence of components of the krill population not identified in net samples during the CCAMLR 2000 Survey.

5. Conclusion

Analysis of the length–frequency distributions of krill taken by scientific nets and Antarctic fur seals at three locations in the Scotia Sea suggests that when comparisons are made at appropriate temporal and spatial scales, Antarctic fur seals provide a view of the krill population structure that is congruent with net samples. There are, inevitably, constraints on both approaches, with net samples providing high spatial resolution but generally covering a relatively limited time period, compared to the lower spatial resolution and greater temporal coverage available from predator samples. Since variability in the regional krill population size structure reflects a combination of the spatial and temporal components of that variability, it is essential to consider different sampling approaches that most appropriately address the different components of this variability. Understanding the regional population dynamics requires information on the size structure of the krill population at a range of scales collected using a range of sampling approaches relevant to those scales. Such information, including transport from source regions and interannual fluctuations in recruitment, is essential for effective management of the commercial exploitation of krill resources.

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